

THE GENERA OF VITACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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VITACEAE A. L. de Jussieu, Gen. Pl. 267. 1789, "Vites," nom. cons.
(GRAPE FAMILY)

Unarmed [rarely armed] woody, sometimes \pm fleshy vines climbing by stem-tendrils opposite the leaves [or rarely tendriless perennial herbs, shrubs, or small sometimes succulent trees]; branches often swollen [or articulated] at the 3-7-lacunar nodes. Leaves alternate [very rarely the upper ones opposite], usually 2-ranked, simple or palmately [rarely pedately] or pinnately compound, petioled [rarely sessile]; stipules small, deciduous [or wanting]. Inflorescences compound cymes, thyrses, or more rarely panicles, borne singly opposite the leaves and sometimes also terminal [rarely only terminal], sometimes provided with a tendril, usually manifestly peduncled, bracteate. Flowers small, regular, usually 4- or 5-merous (except the usually 2-carpellate gynoeceum), hypogynous, pediceled, bi- and/or unisexual (at least functionally), the plants often polygamo-dioecious or -monoecious. Sepals connate, the calyx tube small, saucer- to cuplike. Petals distinct [very rarely connate at base] and spreading or recurved at anthesis, or apically coherent and dropping off as a "cup" at anthesis. Stamens opposite the petals, distinct [very rarely connate into a "staminal tube"], sterile [or very rarely wanting] in $\text{\textit{f}}$ flowers; filaments filiform; anthers introrse [very rarely extrorse], dorsifixed above the base or near the middle, 2-locular at anthesis. Pollen medium sized or rarely small, usually 3-colp-(or)ate, oblate-spheroid to prolate, often rounded-triangular in polar view, reticulate. Nectariferous disc intrastaminal, rarely \pm obscure [or wanting]. Gynoeceum usually 2-carpellate [very rarely 3-8-carpellate].

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syncarpous, usually rudimentary in ♂ flowers; stigma usually small, simple [rarely lobed to parted]; style single, short to long; ovary superior, often variously adnate to disc from base to almost the top, 2[-8]-locular often incompletely so; ovules 2, collateral [rarely ovule solitary] in each locule, ascendent from carpellary margin at base of locule, anatropous, apotropous, 2-integumented, with a thick nucellus. Fruit a 1-4[-6]-seeded berry, usually ± fleshy and juicy. Seed coat usually hard, bony or crustaceous, with an adaxial raphe and abaxial chalaza; endosperm copious, hard-fleshy, rich in protein (aleurone grains) and oil, usually adaxially 3-lobed [rarely unlobed and/or ruminant]; embryo "spatulate," small, straight, ± axial; cotyledons small; radicle elongated, inferior. (Including Leeaceae Dumortier, Anal. Fam. Pl. 21, 27. 1829, nom. cons.) TYPE GENUS: *Vitis* L.

A primarily pantropical family of about 13 genera with some 700 species, a few genera primarily of the North Temperate Zone; four genera in our area.* The genus *Leea* L., of the Old World Tropics, which differs from the rest of the family mainly in its nonclimbing habit, sympetalous corolla, staminal tube, extrorse anthers, lack of a nectariferous disc, and ovary with 3-8 one-ovulate locules, is considered to represent either a subfamily of Vitaceae (Gilg) or a family of its own (Suessenguth, Schultze-Motel).

The genera of the very natural subfam. VITOIDEAE are distinguished primarily by a combination of relative length of style, structure of the nectariferous disc, and configuration of endosperm in cross-section. In some cases, the number of perianth parts and stamens, the character of the corolla (petals free and expanding, or apically connate and forming a "cup"), the inflorescence type, and rarely the character of the tendrils, also are considered to be of generic significance. Since most of the individual generic characters may vary considerably within and form transitions between the genera, generic limits are in some cases somewhat uncertain.

Although the vast majority of Vitaceae are sympodial, tendril-bearing vines, there are some tropical tendrillless species with the stems either monopodial or sympodial.² The occurrence of intermediates between in-

* After this article was in press, L. H. Shinnors recorded (Sida 1: 384. 1964) a collection of *Cayratia japonica* (Thunb.) Gagnep. (*Rylander* 167, 8 July 1963 [SMU]), from a damp, deciduous-forested river bottom at the Delta Primate Research Center of Tulane University, Covington, St. Tammany Parish, Louisiana. This collection "possibly represents an escape from cultivation."

² The Braun-Eichler theory (Troll, pp. 30-32; Suessenguth, pp. 183-190) which regards the shoots of tendril-bearing members of Vitaceae as congenitally formed sympodia, seems at present to offer the most satisfactory explanation of the position of inflorescences and tendrils in this family. Of the other theories (see Eichler, *Blütendiagramme* 2: 375-378. 1878; Suessenguth; Chadefaud), that of Nägeli & Schwendener (*Das Mikroskop* 605. 1867), based on a study of ontogeny, should be mentioned. According to this theory, supported recently by Shah (1962) on the same basis, the tendrils in Vitaceae are extra-axillary lateral branches of a monopodially branched shoot, destitute of subtending leaves. It seems appropriate to quote Troll's comments (*loc. cit.*) on Nägeli & Schwendener's theory. "Consequently, the ontogeny

florescences and tendrils (e.g., inflorescences sensitive to a contact stimulus and performing slight twining movements; those divided into a floriferous part and a tendril; or tendrils bearing a few flowers at the tips of their branches) is ample evidence for regarding the tendrils as modified inflorescences. The tendrils (and inflorescences) are either "continuous" (at each of 3-7 or more successive nodes) or "intermittent" (lacking on every third node) and are either monochasially 2-12-branched, or sometimes once or twice forked, or unbranched. The tendrils attach themselves to the support by twining (coiling) or by adhesive discs developing at the apices of their branches in response to a contact stimulus (e.g., in most of the species of *Parthenocissus*; the monotypic *Pterocissus* Urb. & Ekm.; and some species of *Cissus* and *Tetrastigma* (Miq.) Planch.).

Cross-pollination by insects seems to be the rule, although at least in some monoclinal or polygamo-monoecious species or varieties self-pollination (including geitonogamy) has also been recorded.

Floral anatomical data known for a few genera and species indicate incomplete septation of the ovary and "anatomically parietal" placentation (Kashyap, 1957; Nair & Mani).

Chromosome counts made for eight genera (about 57 species) are $2n = 22, 24, 26, 28, 30, 32, 38, 40, 44, \text{ca. } 45, 48, 50, 52, 60, 72, 80, 96, 98$, suggesting that both aneuploidy and polyploidy have been of importance in the evolutionary development of Vitaceae.

The very characteristic seeds of VITOIDAE make possible the safe determination of fossils of this subfamily. The seeds are usually more or less oblong-obovate or obovate in outline (or sometimes pyriform and distinctly beaked at the micropylar region); the shape in cross section depends upon the number of seeds in a fruit. The seed coat is composed of a thin, outer, parenchymatous membrane and a hard, usually bony, inner layer (sclerotesta). The adaxial (ventral) surface of the sclerotesta exhibits a median cordlike to threadlike raphe, extending from the hilum to the seed apex and onto the convex abaxial (dorsal) side, where it joins a round to linear, depressed to somewhat elevated "chalazal knot." On the adaxial surface the raphe is flanked on either side by a deep groove (an infolding of the sclerotesta) varying in shape and length; the endosperm is consequently deeply three-lobed on the adaxial side. (See FIG. 1.)

The family is closely related to Rhamnaceae, from which it differs mainly in the predominance of sympodial vines, the hypogynous flowers, the predominantly two-ovulate locules, the apotropous ovules, the somewhat different pollen (similar to Araliaceae rather than to Rhamnaceae),

leads to the improbable assumption of 'extra-axillary' branches destitute of subtending leaves, unless it happens that one is entirely willing to attribute the occurrence of such branches to a kind of dichotomous division of the [shoot] apex. By this [assumption of extra-axillary branches], one of the most universal principles of ramification [of the stems] of higher plants would be broken down ['through'] . . . This case impressively teaches what is generally true for congenital processes, that the understanding of these conditions can not be obtained from the ontogeny, [and] that, on the contrary, the latter itself requires explanation through comparison with the fully developed [mature] state." (Translation supplied.)

the type of fruit (berry), the usually lobed or ruminant endosperm, and the "spatulate" (*vs.* "investing") embryo. Together these families constitute the order Rhanales.

It is noteworthy that species of *Tetrastigma*, and perhaps of some other genera of Vitaceae, are the exclusive host plants of the species of *Rafflesia* in Malasia.

Economically the family is most important for the species of *Vitis* (*q.v.*).

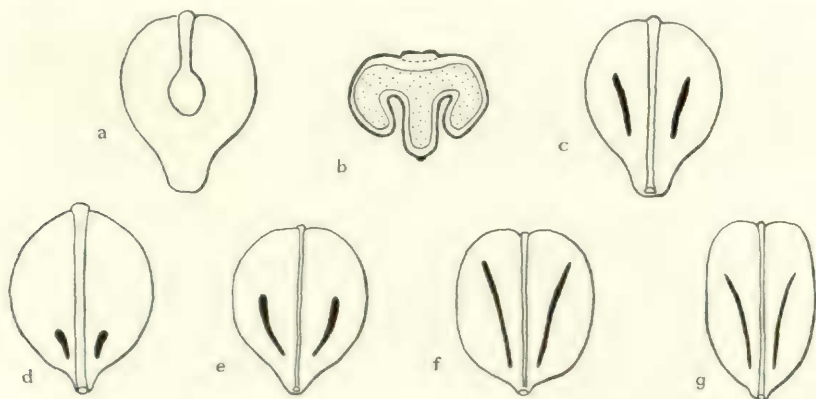


FIG. 1. Diagrams to show characteristic seeds of Vitaceae subfamily Vitoideae with outer membranaceous layer of seed coat removed; relative sizes of seeds modified for ease of comparison. a-c. *Vitis* (subg. *Vitis*) *Labrusca*: a, convex abaxial surface, showing "chalazal knot" with raphe extending to seed apex; b, cross section, showing thick sclerotesta, "chalazal knot," grooves flanking raphe, and endosperm (stippled); c, adaxial surface, showing raphe extending from hilum to seed apex with flanking grooves in black. d-g, adaxial surface of seeds to show variation in raphe and grooves: d, *Cissus incisa*; e, *Ampelopsis arborea*; f, *Parthenocissus quinquefolia*; g, *Vitis* (subg. *Muscadinia*) *rotundifolia*.

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KEY TO THE GENERA OF VITACEAE

General characters: usually woody vines climbing by tendrils opposite the leaves; leaves alternate, simple or palmately 3-5-foliolate, rarely bipinnate; inflorescences opposite the leaves; flowers small, regular, 4-5-merous (except 2-carpellate gynoeceium), hypogynous; stamens opposite the petals; nectariferous disc intrastaminal, conspicuous, rarely obscure; ovary 2-locular, with 2 subbasal, ascendent ovules in each locule; fruits 1-4-seeded berries; seed with a conspicuous abaxial chalazal knot and 2 deep adaxial grooves, one on each side of the raphe.

- A. Petals expanding at anthesis, distinct; inflorescence usually cymose, without a tendril; pith white.
- B. Flowers 4-merous; inflorescence an umbel-like compound cyme (pleiochasium); leaves 3-foliolate, rarely simple. 1. *Cissus*.

- B. Flowers 5-merous.
- C. Nectariferous disc conspicuous, cupular, distinct at least in the upper part; inflorescence a thyrs, usually repeatedly bifurcate and corymb-like, rarely raceme-like; leaves simple or bipinnate; tendrils bifurcate, without adhesive discs. 2. *Ampelopsis*.
- C. Nectariferous disc obscure, reduced and fused with base of ovary; inflorescence a pyramidal cymose panicle with monochasially branched rachis; leaves palmately (3)5-foliolate; tendrils monochasially 3-12-branched, developing adhesive discs at tips of their branches. 3. *Parthenocissus*.
- A. Petals cohering at apex and falling off as a unit at anthesis; inflorescence a panicle, sometimes with a tendril; pith brown; leaves simple. . . . 4. *Vitis*.

1. *Cissus* Linnaeus, Sp. Pl. 1: 117. 1753; Gen. Pl. ed. 5. 53. 1754.

Deciduous [or evergreen] \pm woody, sometimes \pm fleshy [or herbaceous] vines [rarely tendriless perennial herbs, shrubs, or small \pm succulent trees]; tendrils continuous, simple or bifurcate, without [or very rarely with] adhesive discs; roots often tuberous. Leaves simple, unlobed or lobed, and/or palmately 3[-5]-foliolate, membranaceous [to leathery] or \pm fleshy, petioled [rarely sessile]. Inflorescences compound umbel-like cymes (pleiochasia) without tendrils, each opposite a leaf [rarely terminal], continuous, the secondary branches sometimes bifurcate. Flowers 4-merous [exceptionally 5-merous], bisexual [or bi- and unisexual, the plants then polygamo-monoecious], greenish- or creamy-yellow, white, or purplish. Calyx cuplike, indistinctly shallowly 4-lobed to subentire. Petals 4, usually expanding, spreading at anthesis. Stamens 4. Nectariferous disc cuplike, adnate high up on the ovary [or distinct and 4-parted, or replaced by 4 distinct bowl-like glands], the free upper margin \pm 4-lobed or crenate to subentire, spreading or upright. Stigma small; style rather long, \pm filiform; ovary 2-locular, apparently incompletely so (in our species).³ Berries subglobose-ovoid to -obovoid, 5-12 mm. in diameter, dark purple to black, usually 1(2)-seeded, inedible. Seed obovoid, indistinctly beaked at base; chalazal knot linear, on lower part of abaxial face, imperceptibly merging with the narrow, linear, salient raphe running toward seed apex on abaxial and down to hilum on adaxial face; 2 adaxial grooves short, oblong, near base of seed (FIG. 1, d); sides of seed indistinctly very coarsely reticulate. TYPE SPECIES: *C. vitifolia* L., $2n = 26$. (Name from Greek, *kissos*, an ancient name for ivy, applied by Linnaeus to this genus.)

A nearly pantropical genus (exclusive of Hawaii and Polynesia) of nearly 350 species, a few in the warmer parts of the temperate zones. Subgenera *CISSUS* (subg. *Eucissus* Planch.), of pantropical distribution,

³ Flowers of a few random herbarium specimens of *Cissus incisa* and *C. trifoliata*, boiled and dissected, invariably showed ovaries with only a narrow central strip of the partition which bore two collateral ovules on each side at base. Additional material should be investigated before any conclusions are drawn.

and *CYPHOSTEMMA* Planch. (sometimes segregated as the genus *Cyphostemma* (Planch.) Alston), of the Old World Tropics, have been recognized. Three species of subg. *CISSUS* occur in our area.

Cissus incisa (Torr. & Gray) Desmoul., marine-vine, a stout vine with fleshy, three-foliolate or deeply three-parted leaves, usually occurs on limestone in hammocks or in rocky and sandy open woods and on bluffs, from central peninsular Florida to Texas, Arizona, and Mexico, north to Arkansas, Missouri, and Kansas. *Cissus trifoliata* L., of the West Indies, Mexico (?), and northern South America (?), differing in the always three-foliolate leaves with smaller, often flabellate, more regularly toothed leaflets, and smaller fruits, occurs in hammocks in southern peninsular Florida and on the Florida Keys. The very polymorphic, tropical American *Cissus sicyoides* L., with more or less membranaceous, simple, unlobed, medium-sized leaves, and often with long aërial roots, occurs in hammocks, from the Florida Keys northward in peninsular Florida to Polk County. The inflorescences of this species (sometimes also of *C. trifoliata*) frequently are greatly expanded and deformed by a smut, *Mycosyrinx Cissi* (DC.) Beck, the flowers being transformed into elongated subcylindrical formations containing spores of this fungus. The genus *Spondylantha* Presl was based on this monstrosity.

The few published data indicate an "anatomically parietal" placentation in a few investigated Asiatic species (Nair & Mani). Chromosome counts for 12 species are $2n = 22, 24, 26, 28, 32, 44, \text{ca. } 45, 48, 50, \text{ and } 96$, suggesting that both aneuploidy and polyploidy have been of importance in the evolution of the genus.

The genus is closely related to the monotypic Laotian *Acareosperma* Gagnep., and probably to *Cayratia* Juss. The genus is in need of a modern revision.

The tuberous roots of *Cissus trifoliata* are reputedly poisonous. The aërial roots of *C. sicyoides* are locally used in Central America for wattle baskets, and leaves of this species seem to contain saponines and are locally used for washing linen in tropical America.

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2. **Ampelopsis** Michaux, *Fl. Bor.-Am.* 1: 159. 1803; emend. Planchon in A. & C. de Candolle, *Monogr. Phaner.* 5(2): 453. 1887.

Deciduous woody vines; tendrils usually few and scattered [or many and continuous], bifurcate, devoid of adhesive discs. Leaves membranaceous, simple or bipinnate [pinnate or palmate], long-petioled. Inflorescences few- to many-flowered thyrses, each opposite a leaf, continuous, often repeatedly bifurcate and corymb-like, more rarely elongated, raceme-like, the ultimate branches ending in usually umbel-like, crowded, sessile, 3-flowered dichasia. Flowers 5-merous [4-merous in 1 species], bisexual, greenish. Calyx very small, \pm saucer-like. Petals 5, spreading at anthesis. Stamens 5. Nectariferous disc cupular, distinct except the lower part adnate to the ovary, shallowly lobed or crenulate to subentire on the margin. Stigma small, simple; style elongated, slender; ovary 2-locular, apparently incompletely so in our species. Berries subglobular to obovoid, 6-8 mm. in diameter, green, blue, or black, 1-4-seeded. Seed obovate to broadly obovate in outline, convex on abaxial, \pm angular on adaxial side; chalazal knot \pm spatulate, at or below center of abaxial side; raphe narrowly linear, salient on abaxial, threadlike on adaxial surface; 2 adaxial grooves oblanceolate, usually somewhat curved, in the lower half of seed (FIG. 1, e). LECTOTYPE SPECIES: *A. cordata* Michx.; see Britton & Brown, *Illus. Fl. No. U. S. ed. 2. 2*: 509. 1913. (Name from Greek, *ampelos*, grapevine, and *opsis*, likeness, appearance; i.e., having the appearance of the vine, *Vitis vinifera*.)

A genus of about 22 species, of tropical and warm-temperate regions of Asia (19 species, centered in China) and North America (3 species); two indigenous and one naturalized species in our area. *Ampelopsis cordata* Michx., $2n = 40$, a high-climbing, nearly glabrous vine, the leaves simple, ovate, cordate or truncate at base, unlobed or slightly 3-lobed, coarsely and sharply toothed, the berries greenish or bluish, occurs in rich woods and bottomlands from northern Florida to Texas and Mexico, north to southeastern Nebraska, southern Illinois, southern Indiana, southern Ohio, and Virginia. It seems to be closely related to the eastern Asiatic *A. brevipedunculata* (Maxim.) Trautv. (*A. heterophylla* Sieb. & Zucc.), $2n = 40$, a more or less pubescent vine with ovate-cordate, 3-lobed, simple leaves and bright-blue berries, which is cultivated for ornament and is sporadically naturalized in at least North Carolina and Georgia (Small), northward to Ohio and New England. *Ampelopsis arborea* (L.) Koehne (*A. bipinnata* Michx.), pepper-vine, $2n = 40$, generally a high-climbing vine (or sometimes bushy), with bipinnate (or -ternate) leaves, rather small, coarsely toothed or incised leaflets, and dark-purple to black berries, occurs in swampy woods from southern Florida to Texas, north to Oklahoma, Missouri, southern Illinois, and to Virginia and Maryland. It is closely related to *A. orientalis* (Lam.) Planch., of Asia Minor. The relationships of the third North American species, the ternate-leaved *A. mexicana* Rose, of western Mexico (Sinaloa to Guerrero), remain uncertain.

Inflorescences showing transitions to tendrils, with a branch or the peduncle spirally coiled, have been frequently observed in *Ampelopsis cordata*. In at least our species, the septa of the ovary are not connate at the center. The genus appears to be homoploid, $2n = 40$ having been found in the six species investigated.

A close relationship to *Ampelocissus* Planch., *Vitis*, and especially to *Parthenocissus* has been assumed by various authors. The genus is in need of a modern revision.

REFERENCES:

Under family references see BRANDT, LENGERKEN (pp. 343-359), SCHNEIDER (pp. 318-323, 1033, 1034), SUESSENGUTH (pp. 313-315), VATSALA, and VIALA & VERMOREL (1: 68-75. 1910).

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MEEHAN, T. The native flowers and ferns of the United States. vol. 2. v + 200 pp. pls. 1-48. 1879. [*Vitis indivisa* Willd. (= *Ampelopsis cordata*), 21-24, pl. 6.]

3. *Parthenocissus* Planchon in A. & C. de Candolle, *Monogr. Phaner.* 5(2): 447. 1887.

Deciduous [rarely evergreen] high-climbing vines; tendrils intermittent, monochasially 3-12-branched, with [rarely without] adhesive discs at

tips of branches. Leaves palmately [very rarely pedately] (3)5(7)-foliolate, long petioled, leaflets medium sized to large, coarsely toothed, sessile to long petiolulate. Inflorescences usually many-flowered cymose panicles with prolonged monochasially branched rachises [or corymb-like bifurcately branched thyrses], lacking tendrils, opposite the leaves, intermittent, and sometimes also terminal. Flowers 5-merous, bisexual [sometimes also functionally ♂], greenish. Calyx small, cupular, shallowly irregularly 5-lobed. Petals 5, concave, thickish, expanding at anthesis. Stamens 5. Nectariferous disc usually obscure, fused with the ovary base, distinguishable from the ovary by darker color, secretion of nectar, and anatomical structure [or rarely disc evident]. Stigma simple, small; style narrowly conical, short; ovary 2-locular, the septa meeting in the center and apparently not or weakly connate. Berries subglobular, 5–10 mm. in diameter, dark blue to black, often glaucous, 1–4-seeded, inedible. Seed obovate to obovate-suborbicular in outline, convex on the abaxial, angular, ± keeled on the adaxial side; chalazal knot round to short-spatulate, situated in or above the center of abaxial surface, extended to the seed apex into a linear ± salient raphe inconspicuous and threadlike on the adaxial side; 2 adaxial grooves narrow, cracklike, slightly curved, extending nearly from apex to base of seed (FIG. 1, f). LECTOTYPE SPECIES: *P. quinquefolia* (L.) Planch. (*Hedera quinquefolia* L.); see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 511. 1913. (Name from Greek, *parthenos*, virgin, and *kissos*, ivy; an equivalent of *vigne-vierge*, the French name for the type species.)

A genus of about 15 species, of the temperate and tropical regions of eastern Asia and North America, centered in Asia (12 species); one species in our area.

Parthenocissus quinquefolia (*Ampelopsis quinquefolia* (L.) Michx., *A. hederacea* (Ehrh.) DC.),⁴ Virginia creeper, woodbine, $2n = 40$, occurs

⁴ Rehder (1905) presented strong arguments for regarding *Hedera quinquefolia* L. as a species of *Parthenocissus* developing adhesive discs on its tendrils. Consequently he applied *P. quinquefolia* (L.) Planch. to this species. Suringar supported Rehder's interpretation of the type species of the genus with numerous data from the pre- and early post-Linnaean literature. Graebner (1900, 1908, and 1928), however, was of the contrary opinion and applied *P. quinquefolia* to the species without adhesive discs, known at present as *P. vitacea* (Knerr) Hitchc. Rehder's view has generally been accepted by American and European botanists, but a few botanists have adopted Graebner's interpretation. Thus, in his *Catalogus Florae Austriae* (1: 414. 1957), Janchen treats *P. quinquefolia* as a species without adhesive discs on the tendrils, citing in its synonymy *P. vitacea* (Knerr) Hitchc. and *Hedera quinquefolia* L. The species with adhesive discs, generally known as *P. quinquefolia* (L.) Planch., Janchen calls "*P. pubescens* (Schldl.) Graebner (amplif. Janchen)" with "*P. quinquefolia* Rehder, Schneider, Fritsch, Hegi, Mansfeld, non Graebner" and "non *Hedera quinquefolia* L." in synonymy. Made in good faith, but hardly well founded, this action unfortunately returns confusion to the already stabilized nomenclature of the American species of *Parthenocissus*.

Gleason (1947) showed that *Vitis inserta* Kerner, on which *Parthenocissus inserta* (Kerner) Fritsch is based, "is merely a synonym of *P. quinquefolia*." Hence, the correct name for the species known under that name is *P. vitacea* (Knerr) Hitchc.

in hammocks and woods and on rocky banks from Cuba, the Bahamas, and southernmost Florida (including the Keys) north to Maine, Vermont, southwestern Quebec, New York, Ohio, Indiana, Illinois, Wisconsin, Minnesota, and southern Manitoba, west to Texas, and in Mexico and Guatemala (Huehuetenango). The species is variable, and several forms and varieties, mostly horticultural, have been distinguished. The most frequently encountered wild form of var. *quinquefolia* is f. *hirsuta* (Donn) Fern. (*P. hirsuta* (Donn) Small, *P. pubescens* (Schlecht.) Graebn.), with soft-pubescent lower surface of leaflets, young branchlets, and inflorescences. *Parthenocissus quinquefolia* var. *murorum* (Focke) Rehd., differing from the typical variety mainly in tendrils with 8–12 short branches (as against 3–8 elongated branches) and somewhat broader and thicker leaflets, has been recorded at least from Florida, the Bahamas, Cuba, and Mexico. The species is closely related to *P. laetivirens* Rehd., of central China.

Parthenocissus vitacea (Knerr) Hitchc.,⁴ $2n = 40$, which differs from *P. quinquefolia* mainly in the bifurcately branched corymb-like inflorescences (with a tendency toward racemose branching), tendrils usually lacking adhesive discs, and somewhat larger berries and seeds. occupies a range north and west of our area, occurring from Nova Scotia and Quebec to southern Manitoba and Montana, south to New England, Pennsylvania, Ohio, Indiana, Illinois, Missouri, Kansas, New Mexico, western Texas, and Arizona. The closely related *P. heptaphylla* (Buckl.) Britt. ex Small, perhaps a variety or subspecies of the preceding, with (6–)7-foliolate leaves and smaller leaflets, seems to be restricted to central Texas.

The flowers in at least our species are proterandrous, and cross-pollination appears to be the rule. Bumblebees, honeybees, and some other Hymenoptera, Diptera, and Coleoptera have been recorded as pollinators. Chromosome numbers, known in four species, are invariably $2n = 40$. Hybridization (in cultivation, as well as in the wild) between *P. quinquefolia* and *P. vitacea*, assumed by Schneider (p. 316), can not be substantiated at present, since no authentic records of such hybrids have been available.

The genus seems to be closely related to *Ampelopsis*, as well as to *Ampelocissus* and *Vitis*. A modern revision of the North American species.

Suessenguth (p. 312) adopted *P. vitacea* but made a misleading remark. Having questionably placed *Ampelopsis quinquefolia* DC. var. *vitacea* Knerr, Bot. Gaz. 18: 71. 1893, in the synonymy of *P. vitacea* Hitchc., he noted, "fraglich ob hierher gehörig, da für sie Haftscheiben angegeben werden, für *P. vitacea* Hitchcock dagegen nicht." Apparently Suessenguth misunderstood the English description, since Knerr (*loc. cit.* 70) wrote, "The variety does not cling so closely to its support. In fact it is impossible for it to climb a wall or even a tree unless the bark be very rough, owing to the structure of its tendrils. It climbs more like the grape and the clematis . . . On examination the tendrils will be found to be more like grape tendrils, long curling and grasping by recurved tips, rather than short, digitate and clinging by disk-like expansions as in the case of the typical species [typical variety]."

based on field studies, with special regard to the morphology of inflorescences and tendrils, is desirable.

Both eastern North American species and the eastern Asiatic *Parthenocissus tricuspidata* (Sieb. & Zucc.) Planch. (*Ampelopsis tricuspidata* Sieb. & Zucc., *A. Veitchii* Hort.), Boston ivy, $2n = 40$, are valued ornamentals, used especially for covering arbors, rocks, bushes, and walls. Fruits of at least *P. quinquefolia* are said to be poisonous.

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4. *Vitis* Linnaeus, Sp. Pl. 1: 202. 1753; Gen. Pl. ed. 5. 95. 1754.

Deciduous, rarely evergreen, woody vines; bark of main stem and branches usually shreddy and exfoliating, without distinct lenticels, or rarely close, not exfoliating, with numerous lenticels; pith brown, usually interrupted by diaphragms within the nodes, rarely continuous through the nodes; tendrils usually bifurcate, rarely simple, not forming adhesive discs, intermittent, rarely continuous. Leaves simple [rarely palmately compound], often lobed, dentate. Inflorescences panicles (perhaps thyrses), each opposite a leaf, sometimes with a tendril at the apex of peduncle. Flowers 5-merous, fragrant, both bisexual and (at least functionally) unisexual [rarely bisexual only], the plants polygamo-dioecious to trioecious. Calyx very small, saucer-like, or obsolete, slightly 5-dentate to entire. Petals 5, coherent at apex, separating only at base, falling off as a cup at anthesis. Stamens 5, straight in ♂ and bisexual flowers, reflexed and with sterile pollen [or exceptionally wanting] in ♀. Nectariferous disc of 5 flat, ± distinct or coherent glands alternate with the stamens. Gynoecium rudimentary in ♂ flowers; stigma small; style conical, short; ovary 2-locular. Berries globular [to ellipsoid], 5-25 mm. diameter [or more in cultivars], purple to black, more rarely whitish, pink, bronze, or greenish, glaucous or not, 2-locular, 2-4-seeded. Seeds mostly pyriform, ± distinctly beaked at base, more rarely obovate to obovate-oblong and beakless; chalazal knot round to elliptic, mostly in the center of the abaxial side; 2 adaxial grooves deep, rather long, narrow, ± curved in the upper part (FIG. 1, a-c, g). LECTOTYPE SPECIES: *V. vinifera* L., $2n = 38$; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 505. 1913. (Classical Latin name of the vine, *V. vinifera*.)

A genus of nearly 60 species, of temperate and tropical regions of the Northern Hemisphere, centered in China and in eastern North America. Two very distinct subgenera have been recognized, subg. VITIS, $2n = 38$, comprising the vast majority of species, and subg. MUSCADINIA, $2n = 40?$, including three American species. Morphological differences between the subgenera (see below), coupled with different chromosome numbers and a rather strong genetic barrier, seem to favor the generic segregation of subg. MUSCADINIA. Since, however, cytological data are known only in one of the three species of the latter, and the morphological differences can be evaluated only after a thorough study of the related genera, *Muscadinia* is retained here as a subgenus of *Vitis*.

Subgenus VITIS (§ *Euvtis* Planch.). Bark of the main stem and branches shreddy and exfoliating, without distinct lenticels; pith interrupted by diaphragms within the nodes; tendrils forked; infructescences usually elongated, many fruited; seeds usually pyriform, ± distinctly beaked at base, smooth on the abaxial side. About 17 species (or perhaps fewer) in

our area. There is no agreement as to the interrelationships of these; the sequence in which they are mentioned below reflects only increasing area of occurrence, not taxonomic relationship. The species of subg. *VITIS* often intergrade, and their delimitation appears to be rather difficult; hence the species concepts of various authors differ, and the specific status of some species is still uncertain. A thorough taxonomic and nomenclatural revision is needed.

Vitis illex Bailey (*V. cordifolia* var. *sempervirens* Munson), *V. Smalliana* Bailey, *V. sola* Bailey (apparently closely related to and perhaps conspecific with *V. tiliifolia* HBK., of the West Indies, Central America, and northern South America), and *V. Shuttleworthii* House (*V. coriacea* Shuttlew. ex Planch. 1887, not Miq. 1863) are restricted to Florida. *Vitis araneosa* Le Conte (*V. rufotomentosa* Small), the specific status of which is uncertain, ranges from Florida to Louisiana and southeastern Virginia. The Mexican-Texan *V. Berlandieri* Planch., $2n = 38$, and *V. candicans* Engelm., mustang grape, $2n = 38$, seem to occur in our area at least in western Arkansas. *Vitis Lincecumii* Buckley, $2n = 38$, of Texas, Oklahoma, Arkansas, Louisiana, and southeastern Missouri, recently has been recorded from Scott County, Tennessee. *Vitis Baileyana* Munson is found in upland and mountain areas in Alabama and northwestern Georgia, western South and North Carolina, and eastern Tennessee, north to southeastern Virginia, West Virginia, and southeastern Kentucky. The taxonomic status of *V. Lincecumii* and *V. Baileyana* needs further clarification. While Gleason (New Britt. Brown Illus. Fl. NE. U. S. 2: 517. 1952) suggested that both might be not yet fully stabilized species of hybrid origin, Steyermark (Fl. Missouri 1036, 1037, 1040. 1963) reduced them to the synonymy of *V. aestivalis* var. *aestivalis* and *V. vulpina*, respectively. *Vitis palmata* Vahl (*V. rubra* Michx.), $2n = 38$, ranges from northeastern Texas, northern Louisiana, and central Mississippi north to western Oklahoma, central Missouri, southern Illinois and southern Indiana, west to southern Kentucky and western Tennessee. *Vitis rupestris* Scheele, sand-grape, $2n = 38$, has a similar range, but does not seem to occur in Mississippi and Louisiana; reports of this species from Pennsylvania, the District of Columbia, and North Carolina appear to be based on introductions and escapes.⁵

Five additional species of subg. *VITIS* are of wide distribution in eastern North America: *Vitis vulpina* L. (*V. cordifolia* Lam.), frost-grape, chicken-grape, $2n = 38$; *V. Labrusca* L., fox-grape, $2n = 38$; *V. aestivalis* Michx., summer-grape, pigeon-grape; *V. cinerea* Engelm. ex Millard (including var. *cinerea*, graybark-grape, $2n = 38$, and var. *floridana* Munson, sometimes regarded as a distinct species, *V. Simpsonii* Munson); and the most widely distributed species of North America, *V. riparia* Michx. (*V. vulpina* of authors, not L.), frost-grape or river-bank-grape,

⁵ In his *Spring Flora of the Dallas-Fort Worth Area, Texas*, Shinnars stated, "The name of this species is misapplied by Fernald and Rehder to plants extending north through and far beyond our area." Unfortunately, the basis for this statement was not explained.

which occurs from New Brunswick and Quebec to Manitoba and Montana, south to Virginia, Tennessee, Arkansas, Texas, and New Mexico. *Vitis argentifolia* Munson (*V. aestivalis* var. *argentifolia* (Munson) Fern.; *V. bicolor*, of authors) has a range similar to that of *V. aestivalis* and is usually regarded as a variety of it. Since both seem to occur together within nearly the same range, it appears to be more appropriate to regard *V. argentifolia* either as a form of *V. aestivalis* or as a distinct species. The latter solution seems preferable until further study clarifies the problem.

Subgenus MUSCADINIA (Planch.) Rehd. (*Muscadinia* (Planch.) Small). Bark of main stem and branches close, lenticellate, not exfoliating; pith continuous through the nodes; tendrils simple; infructescences very short, few-fruited; seed obovate to oblong-obovate, scarcely beaked, usually transversely wrinkled on the abaxial side. A strictly American subgenus of two or three species, in the southeastern United States, the West Indies, and Mexico; two species in our area.

Vitis rotundifolia Michx. (*M. rotundifolia* (Michx.) Small), muscadine, southern fox-grape, scuppernong, $2n = 40$, occurs in hammocks, swamps, open woods, thickets, and riverbanks, from southern Florida to Texas, northward, mostly on the Coastal Plain, to Virginia, Delaware, southwestern West Virginia, southeastern Kentucky, Tennessee, extreme southeastern Missouri, and Oklahoma. Leaves in this species are distinctive but rather variable; berries are subglobular, 12–25 mm. in diameter, with thick, tough, purple-black to bronze (in the cultivar 'Scuppernong') skin and tough, sweet pulp with a characteristic musky flavor. Long aerial roots are often present. This species is highly resistant to virus and fungal diseases and insect pests, especially to phylloxera and nematodes. *Vitis Munsoniana* Simpson ex Munson (*M. Munsoniana* (Simpson ex Munson) Small), closely related to and differing from the preceding mainly in the sour, not musky-flavored, black, persistent berries, 8–15 mm. in diameter, with a tender skin and pulp and smaller seeds, is found in hammocks and scrub, in peninsular Florida and Georgia, on the Florida Keys, and in the Bahamas. The leaves, very similar to those of *V. rotundifolia*, are said to be persistent, at least in southern Florida. *Vitis Popenoei* Fennell (*V. vulpina* var. *yzabalana* S. Wats.), of Mexico (Veracruz) and Guatemala (Izabal), seems to be a distinctive species closely related to *V. rotundifolia*. However, fruits and seeds, cytology, and distribution of this species need to be studied. Records of *V. rotundifolia* from Mexico apparently are referable to *V. Popenoei*.

Although the flowers in the genus usually are 5-merous, the number of floral parts (petals and stamens) may vary from three to six (nine), the gynoecium, however, being usually 2-, rarely 3-carpellate (in 6(9)-merous flowers). While most of the cultivars, especially of *Vitis vinifera*, possess bisexual flowers, the wild species usually have bisexual, functionally pistillate, and staminate flowers, the latter with rudimentary gynoecium. Regarding the distribution of sexes, the plants may be polygamo-dioecious (androdioecious; rarely gynodioecious in some cultivars) or trioecious,

more rarely dioecious (with only staminate and functionally pistillate flowers). Cross-pollination seems to be the rule, although in many cultivated varieties with bisexual flowers self-pollination also occurs. Data on pollinating agents of our species are few, but bees seem to be most important.

Chromosome numbers, known in 21 species and numerous cultivars, are invariably $2n = 38$ in the species of subg. *Vitis*, and $2n = 40$ in *V. rotundifolia*. Polyploidy within the genus is rare, and $2n = 57$ and 76 have been found in a few cultivars of *V. vinifera*. "So it is to be considered that speciation in this genus is achieved by intrachromosomal variations brought about by accumulation of genic differences" (Vatsala).

Although wild hybrids have rarely been recorded, the species of subg. *Vitis* hybridize freely, and numerous, sometimes complex, artificial hybrids between *Vitis vinifera* and some North American species, as well as between some of the latter, have been produced. There seems to be, however, a genetic barrier between the species of the subgenera. While the cross *V. (Muscadinia) rotundifolia* ♀ × *V. vinifera* ♂ has always been unsuccessful, the reciprocal cross resulted in a highly sterile F_1 ($2n = 39$). Two such hybrids have recently been made fully fertile by chromosome doubling with colchicine, and a small population of tetraploids has been raised from the artificial amphiploids (cf. Dermen, 1964). A complex triploid ($2n = 59$) hybrid, (*V. Lincecumii* × *Labrusca* × *vinifera*) ♀ × *V. rotundifolia* ♂, which bears only staminate flowers, has been produced.

A close relationship with *Ampelocissus* and a more distant one with *Ampelopsis* and *Parthenocissus* have been assumed by various authors. According to Levadoux, Boubals, and Rives, "In the family of Vitaceae, it is possible to distinguish a comparium containing the genera with $2n = 40$ chromosomes [*Ampelocissus*, *Ampelopsis*, *Parthenocissus*, and *Vitis*]. In this comparium there appears a remarkable exception, the cenospecies *Euvtis* [*Vitis* subg. *Vitis*] to which nearly all the cultivated vines belong, and which is characterized by a chromosome number of $2n = 38$. The linnean species, traditionally differentiated within this cenospecies, are ecospecies between which no genetical barrier can be observed."

The genus is of great economic importance for the edible fruits from which raisins, grape juices, and wines are made. The horticultural varieties of economic importance have originated from *Vitis vinifera* (including extremely numerous cultivars), *V. Labrusca* (e.g., cultivars 'Concord', 'Champion', 'Chautauqua', and others, collectively known as *V. labruscana* Bailey), *V. aestivalis*, and *V. riparia*, and from crosses between certain of these species. In the United States, cultivars of *V. vinifera* are restricted to the Mediterranean-type climate of California; but numerous cultivars derived from hybrids of *V. vinifera* with cultivars of the hardy American *V. Labrusca* are widely grown under the climatic conditions of the eastern United States. All of the latter have a characteristic aroma and produce wines quite different from those from *V. vinifera*. Within the range of *V. rotundifolia* its cultivars are widely grown for the fresh

fruit used for home and local consumption and in the production of a distinctive wine.

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- The vast number of references has been reduced here primarily to those either of general interest or dealing specifically with the southeastern United States. Under family references see especially ADKINSON, ARBAUMONT, BEILLE (pp. 105, 107-109), BOUBALS (1959; 1961), BRANDT, DARWIN (pp. 79-83), KIRCHHEIMER (pp. 1-9, 118-129), NAIR & MANI, SCHNEIDER (pp. 301-312, 1032, 1033), SUESSENGUTH (pp. 283-299; bibliography, pp. 174-179, 283, 284, 296, 297-299, and 334-337 [cultivars]), TROLL (pp. 30-32, 627, 628), VATSALA, and VIALA & VERMOREL (especially 1: 109-718. *pls.* 1-70. 1910).
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